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Comparison of *Sporormiella* dung fungal spores and oribatid mites as indicators of large herbivore presence: evidence from the Cuzco region of Peru

Alex J. Chepstow-Lusty, Michael R. Frogley and Anne S. Baker

A. J. Chepstow-Lusty*

Department of Geography, University of Sussex, Brighton BN1 6DL, UK

e-mail: alexchepstow@gmail.com

M. R. Frogley

Department of Geography, University of Sussex, Brighton BN1 6DL, UK

e-mail: m.r.frogley@sussex.ac.uk

A. S. Baker

Department of Life Sciences, Natural History Museum, London SW7 5BD, UK

e-mail: a.baker@nhm.ac.uk

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* corresponding author

Abstract

The ability of sedimentary proxies (especially dung fungal spores) to reflect the past presence and density of large herbivores on a landscape has been receiving increasing scrutiny. Here we examine the *Sporormiella* spore record from a well-dated, multi-proxy, highly organic sedimentary record from the small lake basin of Marcacocha in the Cuzco region of Peru. The basin, a wetland since *ca.* AD 1840, existed as a small lake for at least 4000 years prior. Previous work at Marcacocha has shown that changes in herbivore densities reflect the abundances of oribatid mites preserved in the lake sediments. This study tests the assumption that both the *Sporormiella* and the oribatid mite records responded in broadly the same way to changes in herbivore densities over the past 1200 years.

Analysis reveals a very low covariance between concentrations of *Sporormiella* spores and the two major components of the oribatid mite assemblage: a single aquatic species of *Hydrozetes* and a less abundant, wider grouping comprising members of the mostly terrestrial superfamily Ceratozetoidea (referred to as the ‘ceratozetoids’). Variations in the *Hydrozetes* assemblage clearly dovetail with known historical events, including the massive decline of indigenous and camelid populations following the collapse of the Inca Empire in the mid-sixteenth century. Comparison with other environmental proxies from the Marcacocha sequence, including diatoms and charophyte oospores, suggests that the ceratozetoids appear to reflect increasing terrestrialization. In contrast, although the *Sporormiella* record indicates the presence of livestock, it fails to register the major historical changes in herbivore presence, though reflects well episodes of lake-level lowering. In small lake settings, therefore, the use of *Sporormiella* to estimate the density of herbivores in the catchment might be considered a relatively blunt instrument when compared with some other indicators.

1. Introduction

The use of preserved coprophilous dung fungal spores as a proxy to indicate the presence of large herbivores on the landscape in the past has become standard practice for many researchers. Whilst the technique has proven especially powerful in analysing patterns of megafaunal extinction (e.g. Burney et al. 2003; Gill et al., 2009; Rule et al., 2012; Rozas-Davila et al., 2016), other workers have used it to estimate livestock densities and the effects of grazing pressure (e.g. Davis and Schafer, 2006; Mazier et al., 2009; Etienne et al., 2013; Gill et al., 2013, Baker et al., 2016). The fungal spores used in these studies are most commonly *Sporormiella*- or *Sordaria*-types and are usually recovered from sedimentary settings, such as cored lake sediments, bogs and forest soils.

In recent years, however, the range of abiotic factors that can influence taphonomic processes in sedimentary settings has been subject to increasing scrutiny because of their potential impact on spore preservation and representation (Baker et al., 2013; Dodson and Field, 2018). For example, a study of modern sediments from a suite of different-sized lakes in Florida by Raper and Bush (2009) suggested that proximity of the core site to the shoreline was important. *Sporormiella* spores are poorly dispersed (Ahmed and Cain, 1972; Davis and Shafer, 2006), a fact reflected in Raper and Bush's (2009) study by higher concentrations of spores occurring in near-shore lacustrine muds (< 20 m from the lake margin) compared with more distal sampling sites. These results were corroborated by a similar study conducted in southern Brazil (Raczka et al., 2016). The implication here is that lake-level history could be a more important control on spore abundance than the presence or absence of herbivores, depending on the location of the sampling site. That said, other studies have shown a more complex relationship between spore concentrations and the distance to the shore, largely because the bathymetric characteristics of some lakes can lead to sediment focusing during deposition and/or flooding events (Parker and Williams, 2011; Etienne et al., 2013). In the case of soil profiles, studies have shown that the local hydrology of the site can also be important: too dry, and the dung may dessicate before the spores can germinate; too wet, and the dung might quickly disintegrate, also preventing germination (Robinson et al., 2005; Wood and Wilmschurst, 2012). Other environmental factors, such as the direct or indirect effects

of grazing, might also impact fungal spore assemblages (e.g. Blackford and Innes, 2006).

In order to help circumvent some of these potential issues, *Sporormiella* records are often analysed in conjunction with other palaeoenvironmental proxies indicative of landscape change, including charcoal remains (e.g. Burney et al., 2003) and palynological evidence of pastoral practices (e.g. Mazier et al., 2009). However, these proxies largely record a response to anthropogenic activity and so are not directly related to herbivore presence, either locally or regionally. To address this issue, the use of vegetation dynamics analysis to investigate direct evidence of herbivory has shown considerable potential, though initial studies have largely been limited to grassland habitats where the palynological footprint is likely to be better defined (Gill et al., 2013). There is still a need, therefore, for other proxies to be developed that directly reflect animal presence and/or density on the landscape and can, at the same time, help to interpret the *Sporormiella* record.

One possible solution might be provided by oribatid mites (class Arachnida, subclass Acari, order Sarcoptiformes, suborder Oribatida), mainly terrestrial microarthropod detritivores occupying a variety of soil and arboreal habitats, with a few aquatic representatives (Schatz and Behan-Pelletier, 2008). The potential of oribatids as palaeoclimatic and palaeoecological proxies was recognized over 50 years ago (Frey, 1964) and they have been used in a variety of studies since (reviewed in Erickson and Platt, 2013). In both areas, however, analyses are hindered by the difficulty of obtaining specimen identifications and also to a lack of ecological knowledge about extant populations. The latter is important because oribatid behaviour and habitats have evidently not changed significantly over time and so parallels can be drawn between conditions now and when fossil representatives were alive (e.g. Schelvis, 1992; Hodgson and Convey, 2005). Well-sclerotized oribatid mite remains preserve well in waterlogged sediment, although structures that carry important taxonomic characters (most commonly the legs), are often missing. Factors affecting numbers and diversity of extant mites are complex. The fauna in the upper soil layer and overlying herbage may be influenced by seasonal factors such as temperature and precipitation (van Nieuwenhuizen et al., 1994), but species have also shown varying responses when different types and amounts of manure were added to their habitat (Seniczak et al., 2016a). In the right setting, therefore, the potential exists

for the same environmental driver (livestock density) to directly influence two different proxies: oribatid mites and *Sporormiella* spores.

In order to test such a relationship we present here a direct comparison of oribatid mite and *Sporormiella* data from a well-dated sedimentary sequence derived from the lake basin of Marcacocha in the central Peruvian highlands (Figs. 1 and 2). Previous work has established that first order changes in oribatid mite abundances at this site (for at least the last 1200 years) in part reflect excrement-derived nutrient flux into the lake and, in turn, fluctuations in animal density on the landscape (Chepstow-Lusty et al., 2007). If the abundance of *Sporormiella* spores and oribatid mites are similarly controlled by large herbivore densities, then our hypothesis is that first order fluctuations in both datasets should track each other.

1.1 Study Site

The lake basin of Marcacocha is located in the Cuzco region of the central Peruvian highlands (Fig. 1). Located at 3355 m above sea-level (asl), the present-day wetland was formerly a small lake (no more than 40 m in diameter) which infilled from *ca.* AD 1830. The basin is situated on a former important pre-Hispanic trading route between the highland trading centres to the west and the Amazonian selva to the east (Fig. 2). During the late 15th and early 16th centuries, at the height of the Inca Empire, caravan trains of up to a thousand camelids would pass through the valley and make use of the lake and surrounding pasture, the best and most extensive on this part of the route (de Acosta, 1986 [1590]; Garcilaso de la Vega, 1966 [1609]). Even today, the wetland area, which is kept perennially moist by glacial melt-water, is important for grazing cattle, goats, sheep and horses.

It has been noted previously that coprophilous spores deposited in smaller basins are likely to better represent the local abundance of herbivores (e.g. Baker et al., 2013; Johnson et al., 2015). Marcacocha is therefore an ideal site at which to test the relationship between *Sporormiella* spores and mite remains. The spatial extent of the lake basin is modest, thereby minimising ‘distance from source’ effects, which is a potential complication posed by relatively large lake basins; it also lacks an inflow or an outflow, so reducing the possibility of sediment focussing.

Sedimentary cores from Marcacocha have yielded a well-dated, high-resolution record of environmental and cultural change spanning the last 4200 years

(Chepstow-Lusty et al., 1996, 1998, 2003) that dovetails with the regional archaeological history (Bauer, 2004). Multi-proxy analysis of the sediments at decadal to sub-decadal temporal resolution has provided detailed datasets that include sedimentology, palynology, geochemistry, plant macrofossils, diatoms and oribatid mite remains (Chepstow-Lusty et al., 2003, 2007, 2009; Sterken et al., 2006).

2. Materials and methods

2.1 Marcacocha sediments and age model

In 1993, a series of overlapping sedimentary cores were recovered from the centre of the Marcacocha basin using a 5 cm diameter Livingstone corer. The overall composite length of the sequence was 8.25 m, consisting of an upper 50 cm horizon of dense peat, underlain by a series of highly organic lake muds (with occasional relatively fine-grained inorganic horizons) to a depth of 6.3 m; sediments below this level consisted solely of gravels (Chepstow-Lusty et al., 1996, 1998, 2003). The uppermost peats were too fibrous to core, so were sub-sampled continuously from a hand-dug pit at 4 cm intervals. A chronology for the sequence was developed using a combination of seven ^{210}Pb determinations (applying the Constant Rate of Supply model) and six radiocarbon dates from bulk organic carbon (five conventional dates and one AMS), demonstrating that the sequence extended back continuously for the past *ca.* 4200 years (Chepstow-Lusty et al., 2007, 2009). (See Fig. S1 and Tables S1 and S2, in SI).

Although both the palynological and mite records at Marcacocha span the entire sequence, this study will restrict itself to a comparison over the uppermost 1.9 m (*ca.* 1200 years). This part of the sequence has the most robust chronology, the highest temporal sampling resolution and the broadest range of existing environmental proxy datasets (Chepstow-Lusty et al., 2009). Moreover, confidence in the primary driver of the oribatid mite signal is also strongest across this interval due to direct comparison with known historical events (Chepstow-Lusty et al., 2007).

2.2 Sporormiella analysis

For the original palynological analyses, volumetric 1 cm³ sub-samples were taken every 4 cm throughout the sequence (corresponding to a temporal resolution of *ca.* every 28 years) and prepared according to the methodology detailed in Chepstow-Lusty et al. (2003). *Sporormiella* spores were not counted at this time, so the original pollen residues were revisited for the purposes of this study and counts made using a Leitz Wetzlar microscope at x 400 magnification. To calculate *Sporormiella* concentrations, the same number of exotics of *Lycopodium* spores were counted as required for the original samples to achieve a sum of more than 300 terrestrial pollen grains and fern spores (except in 20 cases, mostly from the lower part of the sequence, where concentrations were particularly low). The identification of *Sporormiella* spores followed the descriptions and images of Raper and Bush (2009) and Burney et al. (2003), in which the brown medial and terminal spores are distinctly shaped with a thick fungal wall and characteristic s-shaped aperture (Fig. 3). Some authors now treat *Sporormiella* and *Preussia* as synonyms, due to identical diagnostic morphological features and habitat preferences (e.g. Arenal et al., 2004; Dodson and Field, 2018).

An additional 23 sediment sub-samples were prepared during this study in order to increase the temporal resolution at key intervals; *Sporormiella* concentrations in these new samples were calculated relative to a count of 500 *Lycopodium* spores. In all, a total of 68 samples were used to compile the dataset for this study, providing a sampling interval of 1–4 cm and a temporal resolution ranging between *ca.* 7 and 28 years.

2.3 Oribatid mite analysis

The sampling strategy and preparation methodology for mite analysis has been published previously (Chepstow-Lusty et al., 2007). In summary, 146 volumetric 0.5 cm³ sub-samples of sediment were taken through the top 1.9 m of the core at a 1 cm resolution (every 4 cm through the uppermost 50 cm of peats). The sub-samples were then disaggregated in deionized water and the residues hand-picked for oribatid mites under a low-power dissecting microscope. Specimens were briefly air-dried at room temperature to remove excess water, counted and initially mounted in silicon oil on microscope slides, before transferal to cavity slides containing 60 % lactic acid. When necessary, slide mounts were warmed on a hot-plate at *ca.* 70 °C until the mite was transparent enough to see important taxonomic structures. Identifications to

family and genus level were first made using Balogh and Balogh (1992) and then confirmed by consulting more detailed taxonomic literature (e.g., Behan-Pelletier and Eamer, 2003a; Fredes and Martinez, 2016).

In order to achieve a better understanding of the taxonomic composition of the oribatid assemblage at key intervals in this investigation, the remaining sedimentary material from four levels that had already returned high numbers of specimens was analysed (at 67 cm, 78 cm, 107 cm and 151 cm depth). Oribatid counts in these sub-samples were increased to a minimum of 100 individuals, or (in the case of the sub-sample at 151 cm) until all sediment had been exhausted. In addition, the oribatids from the topmost sample of modern peat (collected in 2003) were also analysed in order to provide a picture of the contemporary assemblage composition. Voucher specimens have been deposited in the Arachnida Collection, Natural History Museum, London.

3. Results

Data are shown plotted against depth in Fig. 4; the application of binary splitting techniques (Birks and Gordon, 1985) suggests six main zones.

3.1 *Sporormiella* record

In general, preservation of the *Sporormiella* spores was good, with nearly all found singly. A total of 53 samples (78 %) contained *Sporormiella*; concentrations were commonly < 300 spores/cm³. However, four marked peaks occur in the sequence: in the lowest sample at 188 cm (zone 1; 2909 spores/cm³), at 111 cm (zone 4; 8151 spores/cm³), at 51 cm (11,664 spores/cm³; the zone 5/6 boundary) and in the uppermost 12 cm of the record in the peat deposits (reaching 2027 spores/cm³; zone 6).

3.2 *Oribatid* mite record

Preservation of the mite remains was sufficiently good that identifiable specimens were recovered from 110 of the 144 samples (76 %); no individuals were recovered

from the peat deposits in the upper 50 cm of the sequence (Fig. 4). The lack of leg segments and consequent absence of setal data prevented confirmation of species identities, but the vast majority of remains allowed generic determinations to be made. Although we recognised nine species of oribatid, fossil assemblages were dominated by a single species of the aquatic genus *Hydrozetes* (superfamily Hydrozetoidea; Fig. 3). Concentrations were commonly <10 individuals/cm³ throughout most of the record, though marked peaks occurred at 151 cm (20 individuals/cm³; base of zone 3), 107 cm (58 individuals/cm³; zone 4), 78 cm (46 individuals/cm³; zone 5) and 67 cm (70 individuals/cm³; zone 5). The remaining species mostly belonged to the superfamily Ceratozetoidea (hereafter referred to as ceratozetoids), especially the terrestrial species *Trichoribates* sp. (family Ceratozetidae; Fig. 3) and the aquatic mite, *Zetomimus* sp. (family Zetomimidae). This latter species was originally mis-identified as *Galumna* sp. in Chepstow-Lusty et al. (2007) based on the examination of a photomicrograph. Rarer terrestrial species were from the Crotonioidea (*Nanhermannia* sp.), Oripodoidea (*Zygoribatula* sp. and *Siculobata* sp.), Achipterioidea (*Williamszetes* sp.), Ceratozetoidea (*Pelopsis* sp.) and Oppioidea. Whilst these taxa are a minor component of the overall fossil assemblage, with concentrations commonly only 1–2 individuals/cm³ (zones 2–4), they occur more frequently in those sediments immediately underlying the peats (zone 5). Apart from one immature *Hydrozetes*, all specimens were adults. The modern/surface sample also contained exoskeleton components of six individuals of a mite that does not belong to the Oribatida (viz. order Mesostigmata, family Blattisociidae, *Platyseius* sp.).

In the four sediment sub-samples subjected to extended counts (Fig. 4), *Hydrozetes* sp. was shown to clearly dominate the assemblages by $>90\%$ (Table 1). Conversely, in the most contemporary assemblage (taken from the uppermost peat sample), *Hydrozetes* represents only 29% of the total oribatid mite assemblage, with the ceratozetoids being the dominant group. The dilution of oribatids in this peat sample is also notable: 31 oribatid mites were obtained from 20 cm³ sediment, i.e. 1.55 individuals/cm³, compared with an average of 8 individuals/cm³ in the lake sediments below (in levels where mites occur).

3.3 Comparison of the records

The oribatid and *Sporormiella* concentration datasets are markedly different. Covariance between the *Hydrozetes* and ceratozetoid curves with *Sporormiella* is very low in both cases ($r = -0.09$ *Hydrozetes*; $r = -0.15$ ceratozetoids; $n = 68$).

4. Discussion

The most striking result from this study is the extremely poor covariance between *Sporormiella* spores and oribatid mite concentrations throughout the profile (Fig. 4), even accepting that taphonomic factors are likely to have operated very differently during peat deposition (the upper 50 cm of the sequence) than for the underlying lake sediments. Indeed, if data points from the upper interval are excluded from calculations, covariance between the *Sporormiella* and mite datasets remains very low ($r = -0.1$ *Hydrozetes*; $r = -0.16$ ceratozetoids; $n = 54$). These results strongly suggest that the relationship between the two proxies is more complex than hitherto supposed and that either different drivers are involved or that the proxies respond with different levels of sensitivity.

It is notable that significant historical events relating to land-use change and the corresponding shifts in the density of livestock on the landscape are not reflected by the *Sporormiella* signal. For example, as the Incan empire expanded rapidly in the late 15th and early 16th centuries, agricultural production on the terraced slopes of the Sacred Valley and its tributaries (including the Patacancha) increased significantly, in part to support the growth of the capital Cuzco (Bauer, 2004). However, these highland valleys swiftly suffered major depopulation following the Spanish conquest in 1532, when Old World diseases such as smallpox and measles decimated human communities (Cook, 1981). Livestock also suffered, with approximately two-thirds of the camelids in the Cuzco area dying directly or indirectly from carache, a contagious form of skin disease (de Acosta, 1986 [1590]; Garcilaso de la Vega, 1966 [1609]). Although oribatid mite abundances reflect these well-documented, landscape-scale events, there is no corresponding response from the *Sporormiella* signal, which remains largely muted throughout this period (Fig. 4).

This issue of differential response can be unpicked by considering the taphonomic mechanisms by which the *Sporormiella* spores and oribatids become preserved in the lake deposits together with proxy evidence for changing

environmental conditions at Marcacocha over time. Selected datasets are plotted alongside *Sporormiella* and mite curves in Fig. 5; following Wood and Wilmshurst (2013), biological data are expressed as accumulation rates.

Diatoms provide a powerful tool for exploring lake responses to changing hydrological conditions (Smol and Stoermer 1999). The uppermost 1.9 m of the record at Marcacocha has previously been examined for diatoms at 3–4 cm intervals and found to be dominated by benthic or epiphytic genera including *Anomoeoneis*, *Navicula*, *Craticula*, *Fragilaria*, *Nitzschia* and, especially, *Epithemia*. These taxa are most commonly associated with oligotrophic, shallow fresh-water conditions (Sterken et al., 2006). The Marcacocha diatom record indicates relatively stable, shallow lacustrine conditions from *ca.* AD 1070, with further shallowing occurring from *ca.* AD 1650 until AD 1845, when the lake finally infilled; the top 50 cm of peat were not analysed for diatoms. This environmental history of the lake is broadly corroborated by the charophyte record, consisting of oospores of the genus *Chara* (I. Soulié-Märsche, Pers. Comm.) analysed at 1 cm resolution through most of the sequence (every 4 cm through the top 50 cm of peat). Charophytes prefer clear, nutrient-poor waters and generally decline when conditions become turbid or eutrophic (Krause, 1981; Kufel and Kufel, 2001).

4.1 Factors influencing the presence of *Sporormiella* spores

There are multiple biotic and abiotic factors affecting the representation of dung fungal spores in lake sediments, not just the presence of large herbivores in the local catchment (Parker and Williams, 2011; Perrotti and van Asperen, 2018). One key factor is the poor dispersal capability of the spores, which normally occurs close to ground-level and within a few metres of the surface of the dung source. Part of the reason for this highly localised dispersal is that spores are released clumped together within a gelatinous sheath that attaches easily to vegetation (Ahmed and Cain, 1972; Davis and Shafer, 2006); the presence of fringing vegetation may therefore also present a barrier limiting transport of spores into the lake. Under most circumstances, aeolian mechanisms are likely to be largely ineffectual at this height, though other climatic factors such as changes in precipitation are likely to be important (Jackson and Lyford, 1999; Hernández Trejo et al. 2011).

Moisture levels will not only influence the type and degree of vegetation cover, but also the germination potential of dung fungal spores (Parker and Williams, 2011). Precipitation balance will also directly impact lake-level history, governing both the delivery of sediment into the basin (and ultimately the overall lake ontogeny) and fluctuations in the size of the water body. This latter point is especially important from the perspective of the sedimentary record for the site. As lake-levels decrease, for example, so will the distance between shoreline and the core site. Increases in coprophilous fungal spores in the sequence may therefore be related to a shrinking lake, rather than an increase in livestock densities (and vice versa); this effect is seen in the 18 ka record from the Bolivian lake site of Laguna Khomer Kocha Upper, for example (Williams et al., 2011).

Anthropogenic influences also cannot be ruled out; dung is a valuable resource in these highland communities even today (Winterhalder et al., 1974; Sillar 2000) and its deliberate removal from the landscape for use as fertilizer and domestic fuel could also potentially affect the occurrence of fungal spores in the lake sediments. Ultimately however, given the presence of dung in the near-shore environment, the physical occurrence of coprophilous spores in the Marcacocha sediments is likely to be due to a combination of secondary transport processes, including attachment to grazing livestock and to soil particles and/or vegetation during slope-wash events.

As has already been noted, the *Sporormiella* signal at Marcacocha does not respond as expected to documented historical land-use changes in the basin. Given that the areal extent of the lake is unlikely to have varied significantly over the interval being studied, it is perhaps surprising that there is not a more defined response to changes in animal densities on the landscape. *Sporormiella* accumulation seems to fluctuate around a mean of *ca.* 92.9 spores/cm³/year for most of the lake history prior to infilling (Fig. 5), apart from a few notable exceptions.

Two significant *Sporormiella* accumulation peaks coincide with inferred reductions in lake-levels to shallow, boggy conditions (Fig. 5): at the base of the sequence in zone 1 (*ca.* AD 820-900) and during the infilling of the lake at the zone 5/6 boundary (AD 1840), when spore accumulation reaches its highest value in the entire record (>1947.9 spores/cm³/yr). It is suggested that these conditions would potentially have permitted animals greater access to the surface of what had essentially become a wetland and allowed the accumulation of livestock excrement in closer proximity to the core site. It is probable that this situation would be even more

likely during the most recent phase of lake history (zone 6), when peat deposition would have rendered the surface of the lake site even more accessible to grazing livestock (as it is today).

One other notable peak in *Sporormiella* accumulation is seen in zone 4 at 111 cm (*ca.* AD 1440). This consists of a single sample in which the accumulation rate reaches 815.1 spores/cm³/yr; by comparison, rates from immediately adjacent samples only attain 22.6 and 10.0 spores/cm³/yr. The interpretation of this peak is problematic given that it is not matched by a response in other proxies. If related to a sudden influx of animals on the landscape, it might be expected that other indicators that normally respond to nutrient availability (such as diatoms and charophytes) would also show some response across this interval; however, potential dilution effects notwithstanding, this is not the case (Fig. 5). Moreover, it seems unlikely that this *Sporormiella* peak is related to a sudden decrease in lake volume, since again, other proxy indicators do not support this interpretation. One possibility is that this may represent a discrete, high-energy flooding event, in which surface run-off transported unusually high amounts of organic material from the pasture. However, existing C/N and $\delta^{13}\text{C}$ data across this interval, which might ordinarily be expected to corroborate this interpretation, are inconclusive, possibly a consequence of the sampling resolution employed (Chepstow-Lusty et al., 2007).

4.2 Factors influencing oribatid mites

We hypothesize that there was little or no modification of the study site by long range introduction or migration of taxa and that the mites extracted were deposited more or less *in situ*. This is based on mites' inability to fly and the lack of evidence that mechanisms known to disperse extant species over long distances are likely to be significant in the distribution of those collected. For example, no phoretic relationships have been established, and while it has been shown that if oribatids are dispersed over long distances by wind, it is mainly tree-dwellers that are transported (Pfingstl, 2017); extant representatives of Maracocha taxa inhabit soil, litter and low-growing plants (e.g., Hammer, 1961; Behan-Pelletier and Eamer, 2003b; Ermilov and Gwiazdowicz, 2015). Furthermore, although the major component of the fossil assemblage, *Hydrozetes*, is an aquatic taxon, it is not adapted for swimming and

disperses by crawling. Newell (1945) demonstrated experimentally that adults of two species could also move by a process he called 'levitation', but the movement was vertical rather than horizontal. He hypothesized that levitation in nature might be stimulated by lack of oxygen or food, or by toxic by-products of anaerobic decomposition; field observations have provided some support for this (Fernandez and Athias-Binche, 1986). Less than 1% of known oribatids (about 90 species) are classed as aquatic, i.e., they are active, reproduce and complete their life cycle in or at the margins of freshwater (Schatz and Behan-Pelletier, 2008). Thus, the depauperate fauna at Marcacocha compared to that of a terrestrial site is not unexpected. A similar picture of low species diversity with one dominating species has been recorded in extant oribatid populations in wetland habitats, e.g., a pond shore (Seniczak, 2011) and in bogs (Seniczak et al. 2015).

Species of *Hydrozetes* inhabit freshwater bodies such as ponds, lakes and streams in most regions of the world, usually in association with aquatic plants. They occur below, on and just above the water surface. Fossil specimens have been extracted from many archaeological substrates and used to interpret local climatic and habitat changes. For example, fluctuations in fossil oribatid mite densities from a lake site in New Jersey, USA were shown to reflect changes in nutrient cycling and aquatic productivity associated with Lateglacial and early Holocene climate oscillations (Erickson and Solod, 2007). In the reconstruction of ecological changes at a Late Holocene marsh site in SW Turkey, *Hydrozetes* species extracted from a sediment core were interpreted as indicators of the aquatic and trophic conditions of the site (Schelvis, 2005).

It has been previously established that changes in the concentration of *Hydrozetes* in the Marcacocha sequence reflect first-order shifts in livestock densities in the catchment (Chepstow-Lusty et al., 2007). Confidence in this interpretation is provided by comparison with historical records (de Acosta J, 1590 [1590]; Garcilaso de la Vega, 1666 [1609]; Glave and Remy, 1983). *Hydrozetes* species are detritivores which feed on a variety of decomposing plant matter (Baker, 1985; Athias-Binche and Fernandez, 1986; Fernandez and Athias-Binche, 1986; Covarrubias and Mellado, 1998). Food in the form of plant particles from excrement deposited by visiting camelids could have at least in part been responsible for the increases in numbers seen at Marcacocha. Fragments from desiccating dung blown or washed overground into the lake, or released from deposits left in the water by wallowing animals, would have

boosted food availability. Also, damage to aquatic plants and those in the immediate catchment caused by camelid trampling might have increased the amount of plant decomposition and, in turn, food. Nutrient supply is likely to be especially important given that populations of some members of the genus *Hydrozetes* are thought to expand rapidly by parthenogenesis in response to increasing food supplies (Norton and Palmer, 1991; Norton et al., 1993).

Another hypothesis for changes in *Hydrozetes* numbers is that camelid dung and urine altered the prevailing water quality, again through run-off from the land or direct deposition into the lake. Indeed, data from ecological studies of extant populations show that *Hydrozetes* species vary greatly in their tolerance to different environmental conditions, including pH levels, and amounts of available oxygen, biodegradable organic matter, suspended particles and conductive ions from dissolved salts and inorganic materials (Seniczak, 2011, Seniczak et al. 2013, 2015, 2016b). In general, however, *Hydrozetes* are more likely to reflect more nutrient-rich, eutrophic conditions; compare this with the charophyte and diatom records, which tend to indicate when the lake was shallow and oligotrophic. This broadly antiphase relationship can be seen in Fig. 5 (especially in zones 3, 4 and 5).

Extant representatives of the remaining mite taxa extracted at Marcacocha occur in wet habitats, but are almost all classed as terrestrial because they are inactive when submerged (Table 1); the exception is the genus *Zetomimus*, a ceratozetoid, which is considered to be aquatic as it needs water for all life activities, despite being able to survive dry periods (Behan-Pelletier and Eamer, 2007). Apart from *Siculobata*, the taxa have been previously recorded in Peru from wetland habitats that might have existed previously around the lake basin (Hammer, 1961, Ermilov and Gwiazdowicz, 2015). Most mites originating from terrestrial habitats will enter water bodies via secondary transport mechanisms; localized movement of specimens at Marcacocha could have been the result of run-off from the surrounding landscape or collapse of the lake margin, but introduction by falling from (or with) overhanging branches is unlikely due to the absence of trees and shrubs close to the lake. Because the recorded habitats of these mites match the current environment at Marcacocha, their presence is considered broadly indicative of the level of terrestrialization of the lake basin. Further evidence for this is provided by the occurrence of the mesostigmatid *Platyseius* sp. in the modern surface sample: like the oribatids, these mites live in moist habitats, but are terrestrial.

The paucity of terrestrial specimens through much of the record suggests that only occasional individuals are robust enough to survive the transport process between the pasture and lake; data are therefore generally too sparse to be palaeoenvironmentally useful. However, even in the sub-samples that were subjected to extended faunal counts, it is striking that the terrestrial component of the mite fauna never exceeds 8.1 %, except in the topmost modern peat sample (Table 1), where they dominate (representing 71 % of the assemblage relative to *Hydrozetes*). When lake-levels reduce sufficiently that the environment essentially becomes a wetland (for example), the increased accumulation of other oribatids (notably ceratozetoids) relative to *Hydrozetes* may take on more significance as a ‘terrestrialization’ indicator. This is especially clear from the late sixteenth century onwards and during the period immediately prior to the lake infilling in the mid-nineteenth century (Fig. 5, zone 5).

4.3 Synthesis

On the strength of the evidence presented here, we would argue that the *Sporormiella* signal at Marcacocha is likely to reflect the presence of animals on the landscape, but that the sensitivity of its response is normally insufficient to allow more nuanced fluctuations of livestock populations to be recognised. We would suggest that the *Sporormiella* response at Marcacocha is in line with other wetland sites (e.g. Robinson et al., 2005; Wood and Wilmshurst, 2012), where local hydrological factors at times become more important than animal presence in governing the production and preservation of spores in the sedimentary record. The use of *Sporormiella* might therefore be considered a relatively blunt instrument at such sites in comparison with the *Hydrozetes* signal, which appears to be able to differentiate between different levels of land-use in the basin.

5. Conclusions

At Marcacocha, the *Hydrozetes* mite record accords well with historical livestock changes across the basin, including the major events associated with the rise and fall of the Inca Empire. On the other hand, the remaining oribatid taxa (dominated by the ceratozetoids) appear to provide some indication of increasing terrestrialization

of the lake system. Although *Sporormiella* spores in this setting were able to broadly register the presence of animals within the basin and appeared sensitive to lake-level shallowing, they did not register more subtle livestock fluctuations in response to major historical events. It is likely that local hydrological conditions at wetland sites such as Marcacocha serve to influence taphonomic processes and may potentially mask any response by dung fungal spores to animal presence. This study illustrates that any interpretation of *Sporormiella* spores preserved in such settings should therefore be conducted in conjunction with an understanding of the full range of biotic and abiotic processes that facilitate their deposition in peats and lacustrine sediments.

The use of oribatid mites as livestock density indicators, including widespread genera such as *Hydrozetes*, will continue to be most effective in very small lake basins that are dominated by organic deposition and where an intimate relationship exists with the adjacent pasture. The relatively low number of oribatids recovered from each level in this study was governed by the diameter of the coring equipment employed. To maximise the recovery of sufficient mite remains in future studies, therefore, we would advocate the use of large diameter cores, especially in settings where inorganic input may dilute the sedimentary record. This was the approach adopted by the landmark environmental investigation of mites from the late Glacial-early Holocene sediments at Lake Kråkenes in western Norway by Solhøy and Solhøy (2000). Future studies might also consider incorporating an analysis of ancient DNA (Etienne et al., 2015; Ficetola et al., 2018) and/or promising new biochemical markers linked to faecal matter (e.g. D’Anjou et al., 2012; Guillemot et al., 2016; Gea et al., 2017; Zocatelli et al., 2017), thereby increasing the confidence of inferring livestock presence from the sedimentary record.

Data availability statement

All data discussed in this paper are available from the National Geoscience Data Centre, UK.

Declarations of interest

None.

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Figure captions

Figure 1. Map of Peru and adjacent countries showing Marcacocha in the Cuzco region and other major sites.

Figure 2. General view north-eastwards up the Patacancha Valley over the in-filled lake of Marcacocha (3350 masl). Notice the concentration of pasture adjacent to Marcacocha, the density of surrounding Inca and pre-Incan terraces across the landscape, and the proximity of the Inca road <50 m east, which connects the selva with the sierra. Photo taken in mid-August, 1996 during the height of the dry season.

Figure 3. Photomicrographs of selected specimens from the Marcacocha sequence. **(a, b)** *Sporormiella* spores showing terminal and medial forms respectively, and the characteristic s-shaped suture. Scale bar = 10 μm . **(c, d)** Remains of *Hydrozetes* sp. and the ceratozetoid, *Trichoribates* sp. specimens respectively. Scale bars = 100 μm .

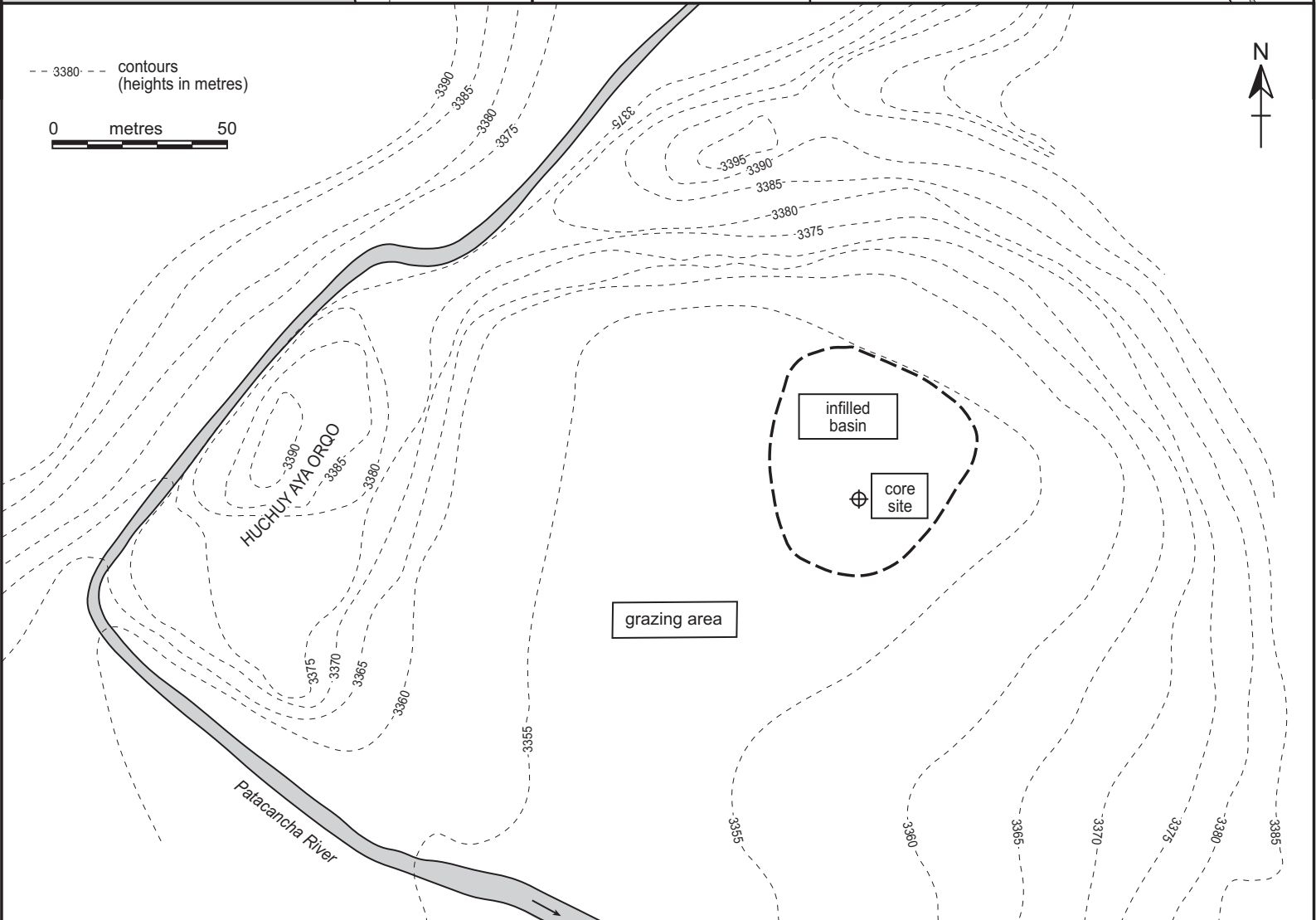
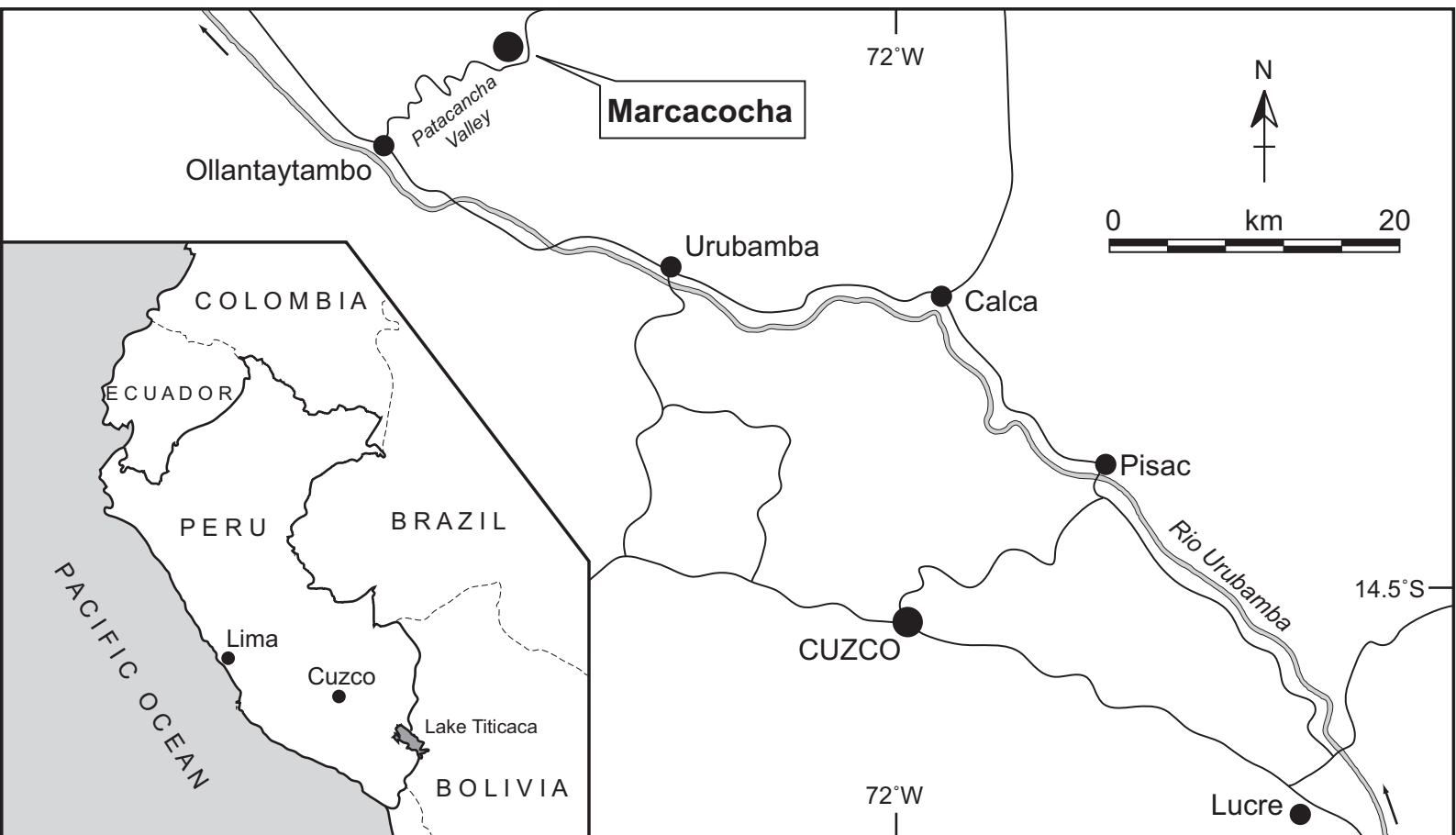
Figure 4. Concentrations (individuals/cm³) of *Sporormiella* spores, *Hydrozetes* sp., ceratozetoids, other oribatids and carbon content (%) plotted against depth. Stratigraphical column shows uppermost 50 cm of peat overlying organic lake muds with occasional relatively fine-grained inorganic horizons (at approximately 50 cm and 143–145 cm depth), with a greater component of inorganic sediments at the base of the sequence. Asterisks (*) mark the four levels subjected to extended oribatid mite counts (see also Table 1). Proxy-derived environmental interpretation from Chepstow-Lusty et al. (2009). Diamonds denote ²¹⁰Pb dates and hatched circles calibrated bulk radiocarbon dates. Calibration was carried out using the SHCal04 dataset (McCormac et al., 2004) in conjunction with version 5.0 of the CALIB calibration program (Stuiver and Reimer, 1993) and are cited as years before present (AD 1950). An age-depth model is provided in SI Appendix 1). Data plotted using *psimpoll* (v. 4.27) (Bennett, 2009).

Figure 5. Multi-proxy diagram with *Sporormiella* spores, *Hydrozetes* sp. and ceratozetoid oribatid mites and selected additional environmental proxies plotted as accumulation (per cm³ per year; diatoms as valves per g per year) against depth. Stratigraphy as described in Fig. 4; proxy-derived environmental interpretation from

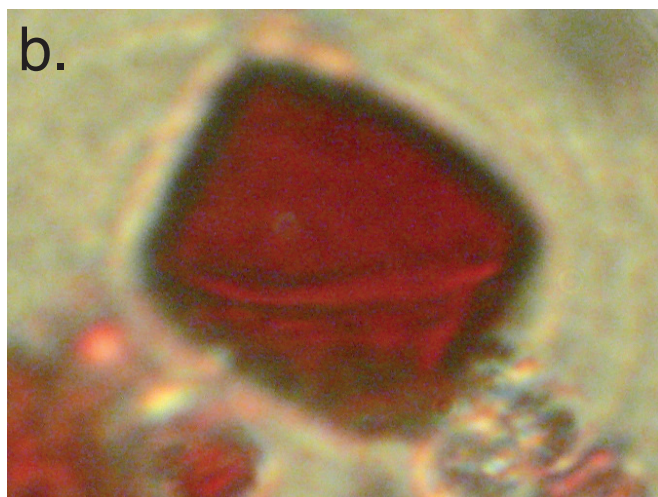
Chepstow-Lusty et al. (2009). Diamonds denote ^{210}Pb dates and hatched circles calibrated bulk radiocarbon dates (see Fig. 4).

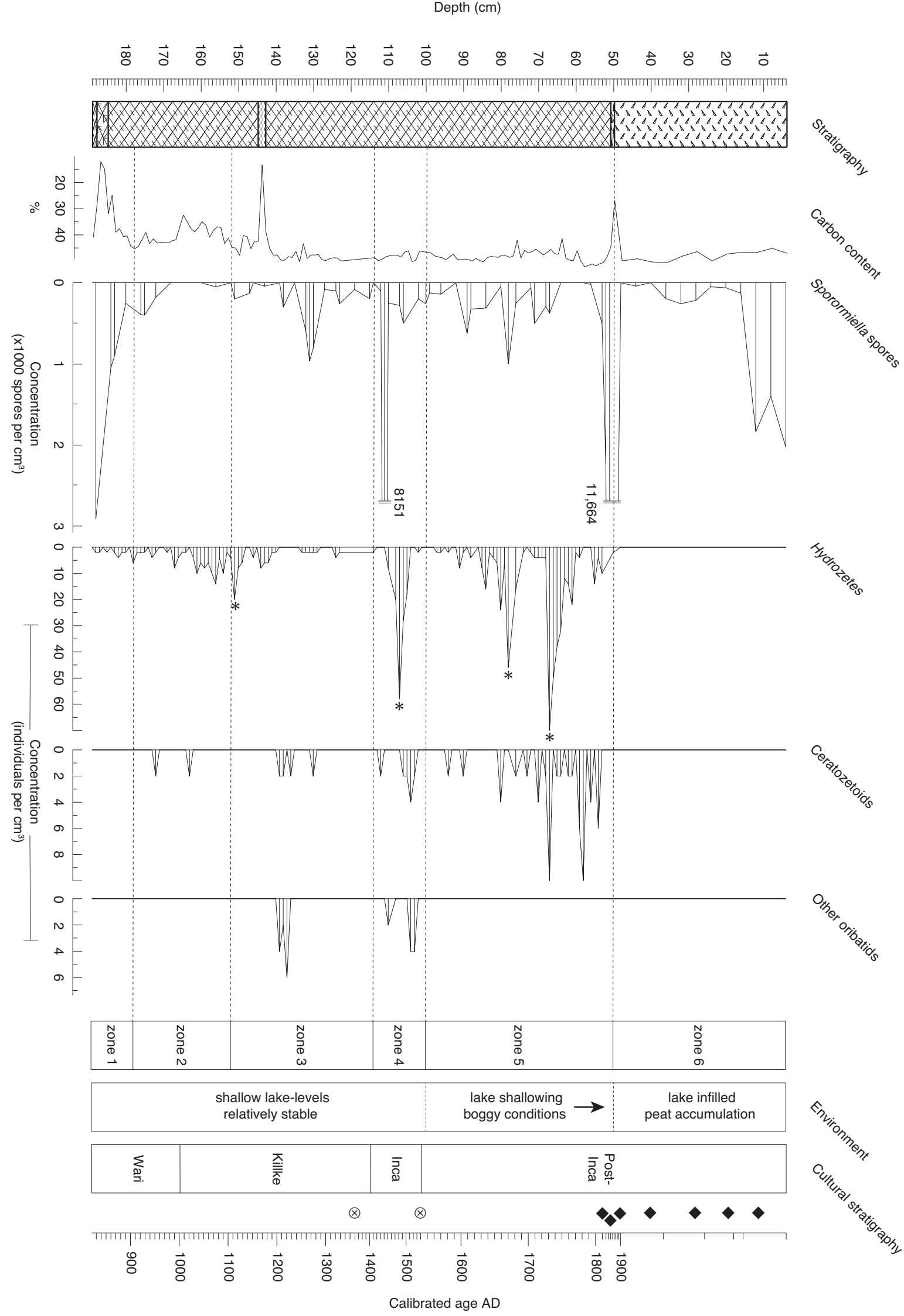
Table 1. Oribatid composition of topmost modern peat sample (collected in 2003) above the infilled lake of Marcacocha and extended counts of oribatid mites from four selected levels in the lake sediment core (67 cm, 78 cm, 107 cm and 151 cm), as indicated in Fig. 4. The markedly reduced *Hydrozetes* sp./total oribatid mite ratio in the topmost peat sample clearly demonstrates increasing terrestrialization. The remains of six mesostigmatid mites were also found in the modern sample, but are excluded here as they are not oribatids. Unidentifiable specimens are probably degraded *Hydrozetes* sp.

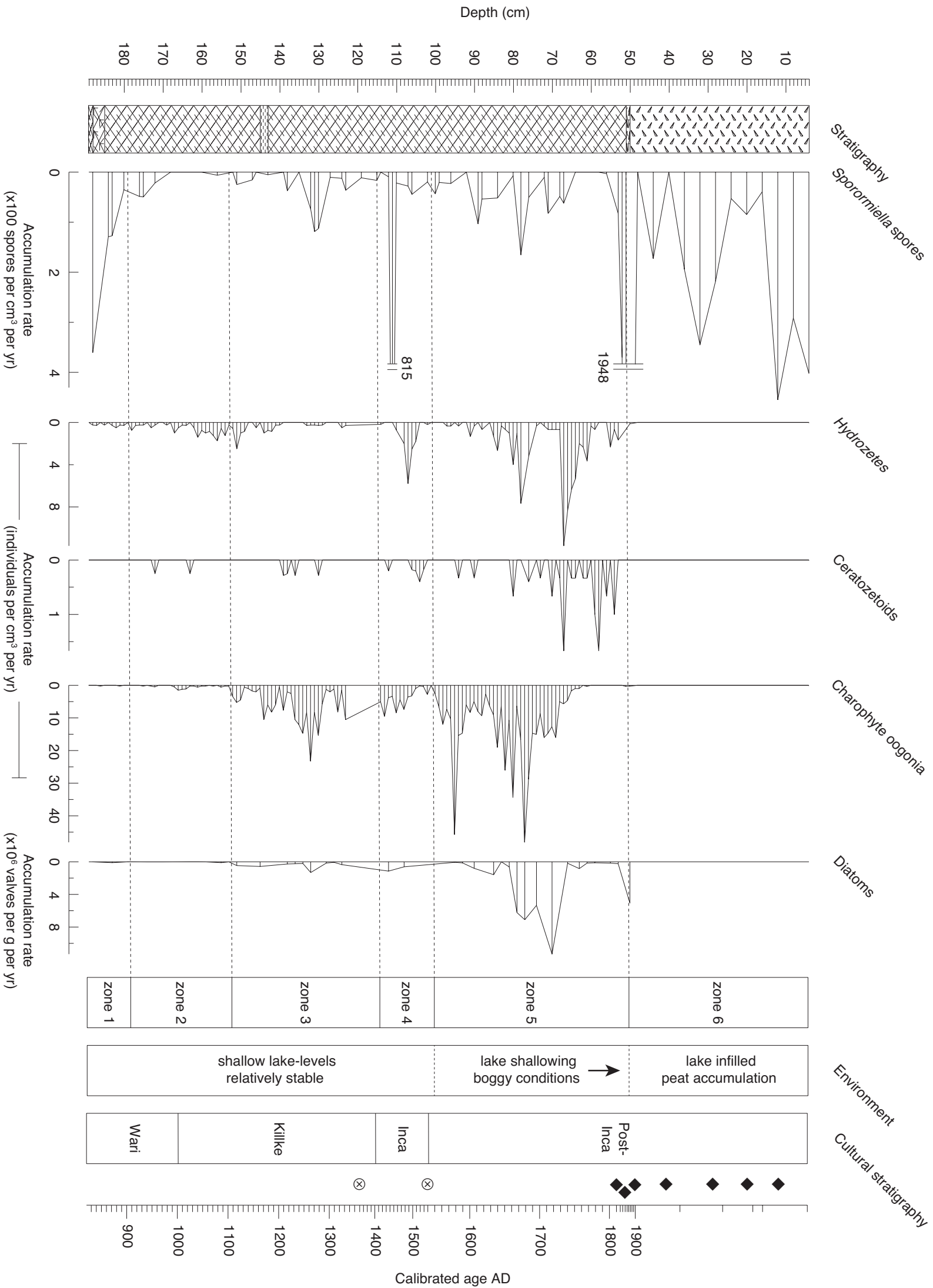
Depth (cm)		Oribatid assemblage	Total no. of oribatids	<i>Hydrozetes</i> / total oribatids (%)	Volume of sediment (cm ³)	Oribatid concentration (individuals/cm ³)
Topmost peat sample	9	<i>Hydrozetes</i> sp.	31	29	20	1.55
	20	Ceratozetoidea (17 Zetomimidae, <i>Zetomimus</i> sp.; 3 Mycobatidae, <i>Pelopsis</i> sp.)				
	2	Crotonioidea (<i>Nanhermannia</i> sp.)				
67	96	<i>Hydrozetes</i> sp.	105	91	2	52.5
	5	Ceratozetoidea (1 Zetomimidae, <i>Zetomimus</i> sp.; 4 Ceratozetidae, <i>Trichoribates</i> sp.)				
	4	<i>Indet.</i> (prob. worn <i>Hydrozetes</i> sp.)				
78	95	<i>Hydrozetes</i> sp.	106	90	3	35.3
	8	Ceratozetoidea (2 Zetomimidae, <i>Zetomimus</i> sp.; 6 Ceratozetidae, <i>Trichoribates</i> sp.)				
	1	Archipteroidea (1 Tegoribatidae, <i>Williamszetes</i> sp.)				
	1	Opplioidea				
	1	<i>Indet.</i> (prob. worn <i>Hydrozetes</i> sp.)				
107	111	<i>Hydrozetes</i> sp.	114	97	2.5	45.6
	3	Ceratozetoidea (1 Zetomimidae, <i>Zetomimus</i> sp.; 2 Ceratozetidae, <i>Trichoribates</i> sp.)				
151	34	<i>Hydrozetes</i> sp.	37	92	3.5	10.6
	3	Ceratozetoidea (2 Zetomimidae, <i>Zetomimus</i> sp.; 1 Ceratozetidae, <i>Trichoribates</i> sp.)				











Supporting Information: Appendix S1

Comparison of *Sporormiella* dung fungal spores and oribatid mites as indicators of large herbivore presence: evidence from the Cuzco region of Peru

Alex J. Chepstow-Lusty, Michael R. Frogley and Anne S. Baker

A. J. Chepstow-Lusty*

Department of Geography, University of Sussex, Brighton BN1 6DL, UK

e-mail: alexchepstow@gmail.com

M. R. Frogley

Department of Geography, University of Sussex, Brighton BN1 6DL, UK

e-mail: m.r.frogley@sussex.ac.uk

A. S. Baker

Department of Life Sciences, Natural History Museum, London SW7 5BD, UK

e-mail: a.baker@nhm.ac.uk

Age-Depth model for the Marcacocha sequence

An age-depth model for the Marcacocha sequence (Fig. S1) was developed using a combination of seven ^{210}Pb determinations (Table S1) and six calibrated radiocarbon dates from bulk organic carbon (five conventional dates and one AMS) (Table S2). All dates have been published previously (Chepstow-Lusty et al., 2007, 2009).

Figure S1. Age-depth model for the Marcacocha sequence using an error-weighted smooth spline (black line; smoothness set at 0.3), plotted using *clam* v2.2 (Blaauw, 2010). The probability distributions of calibrated ^{14}C ages are shown in blue and ^{210}Pb age estimates (top part of the model) are shown as red crosses; see Tables S1 and S2. The grey envelope denotes the 95% confidence interval (based on 1000 iterations).

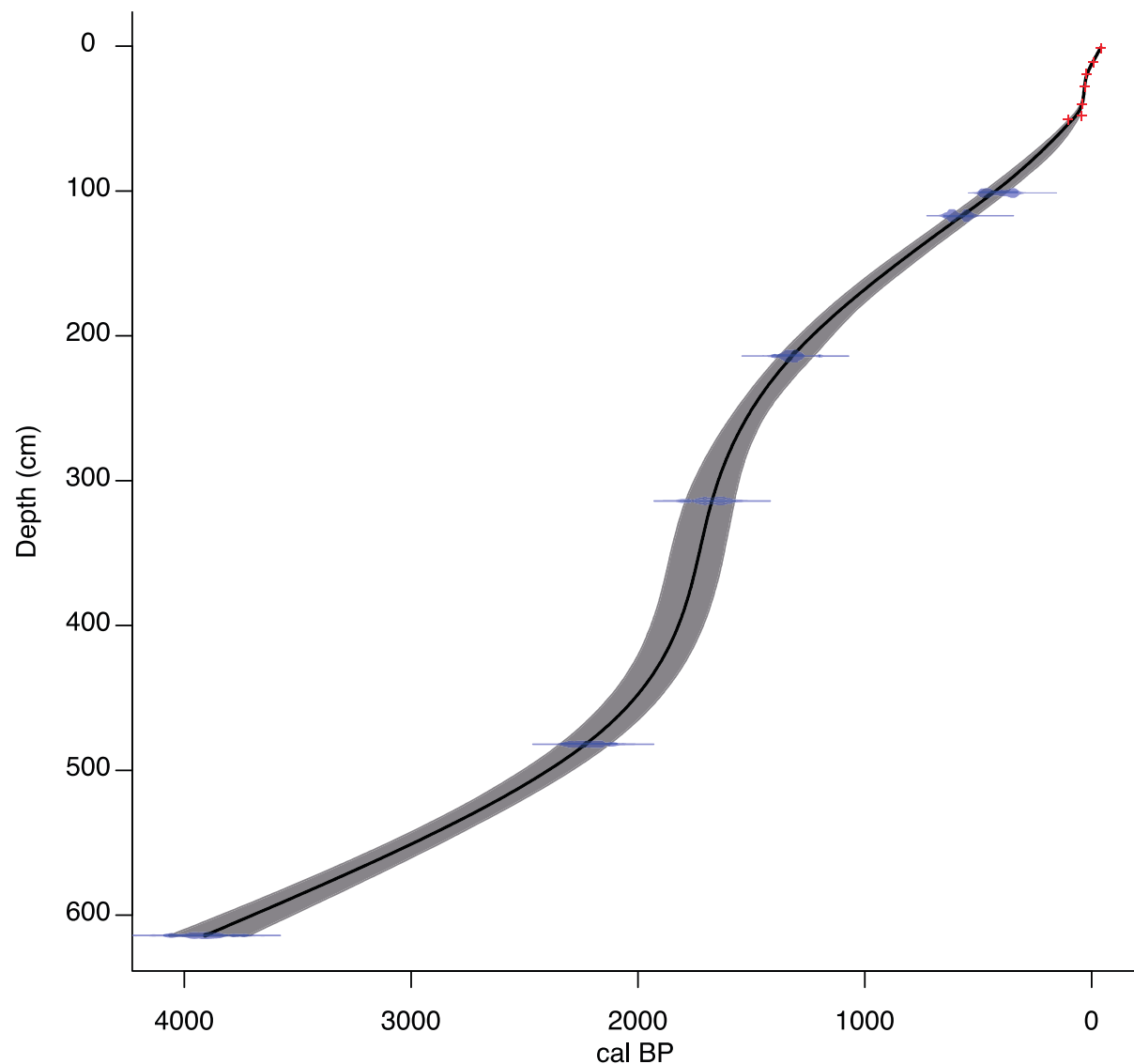


Table S1. ^{210}Pb age estimates for Marcacocha (from Chepstow-Lusty et al., 2007) derived using the Constant Rate of Supply model. Determinations were carried out by A. Cundy (University of Southampton) and followed Flynn et al. (1968).

Depth (cm)	Calendar date
0–2	AD 1991 \pm 0.1
10–12	AD 1958 \pm 0.1
18–20	AD 1926 \pm 0.4
27–29	AD 1918 \pm 0.5
39–41	AD 1907 \pm 0.4
47–49	AD 1905 \pm 2.9
50–51	AD 1845 \pm 8.3

Table S2. Bulk radiocarbon dates from Marcacocha (from Chepstow-Lusty et al., 2009). Calibration was carried out using the SHCal04 dataset (McCormac et al., 2004) in conjunction with version 5.0 of the CALIB calibration program (Stuiver and Reimer, 1993) and are cited as years before present (AD 1950).

Depth (cm)	Laboratory Reference	^{14}C age (yr BP)	Median calendar date		Calibrated date
101–102	Beta 190482	400 \pm 40	AD 1540	1 σ	AD 1458 – AD 1510 (54%) AD 1554 – AD 1556 (1%) AD 1574 – AD 1621 (45%)
				2 σ	AD 1454 – AD 1626 (100%)
115–123	Q-2917	620 \pm 50	AD 1360	1 σ	AD 1315 – AD 1357 (52%) AD 1381 – AD 1419 (48%)
				2 σ	AD 1295 – AD 1437 (100%)
210–218	Q-2918	1,460 \pm 50	AD 630	1 σ	AD 568 – AD 678 (100%)
				2 σ	AD 440 – AD 485 (3%) AD 537 – AD 775 (97%)
310–318	Q-2919	1,805 \pm 50	AD 280	1 σ	AD 138 – AD 199 (20%) AD 206 – AD 403 (80%)
				2 σ	AD 30 – AD 37 (1%) AD 51 – AD 543 (99%)
478–486	Q-2920	2,245 \pm 50	BC 240	1 σ	BC 384 – BC 160 (95%) BC 133 – BC 117 (5%)
				2 σ	BC 479 – BC 470 (<1%) BC 414 – BC 33 (99%) BC 36 – BC 52(<1%)
610–618	Q-2921	3,650 \pm 60	BC 1960	1 σ	BC 21374 – BC 1754 (100%) BC 2430 – BC 2425 (<1%)
				2 σ	BC 2401 – BC 2381 (<1%) BC 2348 – BC 1607 (99%) BC 1572 – BC 1559(<1%) BC 1548 – BC 1540(<1%)

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